

The absence of reward induces inequity aversion in dogs

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Summary

One crucial element for the evolution of cooperation may be the sensitivity to others' efforts and pay-offs in comparison to one's own costs and gains. Inequity aversion is thought to be the driving force behind unselfish motivated punishment in humans constituting a powerful device for the enforcement of cooperation. Recent research indicates that non-human primates refuse to participate in cooperative problem-solving tasks if witnessing a conspecific obtaining a more attractive reward for the same effort. However, little is known about non-primate species although inequity aversion may also be expected in other cooperative species. Here, we investigated whether domestic dogs show sensitivity towards the inequity of rewards received for giving the paw to an experimenter on command in pairs of dogs. We found differences in dogs tested without food reward in the presence of a rewarded partner compared to both a baseline condition (both partners rewarded) and an asocial control situation (no reward, no partner), indicating that the presence of a rewarded partner matters. Furthermore, we showed that it was not the presence of the second dog but the fact that the partner received the food that was responsible for the change in the subjects' behaviour. In contrast to primate studies, dogs did not react to differences in the quality of food or effort. Our results suggest that other species than primates show at least a primitive version of inequity aversion, which may be a precursor of a more sophisticated sensitivity to efforts and pay-offs of joint interactions.

Introduction

Recent studies investigating human cooperation suggest that aversion to inequity may account for much of the variation observed in the data [1]. Inequity aversion is defined as partners resisting inequitable outcomes. In humans, it seems to be based on the simultaneous evaluation of their costs and gains in comparison to those of their partner. It has been suggested that comparing one's own pay-off and effort during cooperation with those of others and reacting negatively to an unequal reward distribution in regard to the effort invested was crucial for the evolution of cooperation [2]. If an individual responds to a disadvantageous reward distribution, it would likely increase its relative fitness compared with those who do not [3]. A simple version of inequity aversion concerns dyadic relationships rather than third-party intervention, thus it does not imply an interest in inequity that exists among other people but is based solely on the subject's own efforts and material payoff relative to the investment and payoff of others.

Until recently, it has been thought that sensitivity towards unequal reward or effort distribution is a uniquely human asset. However, several experiments carried out with capuchin monkeys (*Cebus apella*)[4] and chimpanzees (*Pan troglodytes*)[5] suggest otherwise (but see [6-8]). In these experiments, scientists have attempted to model social situations in which they can test an animals' sensitivity to inequity without requiring cooperation. In the initial study, Brosnan and colleagues [4] used an experimental set-up, whereby an animal had to exchange a token with the experimenter to obtain a food reward. They found that, if tested with a partner in visual contact, the monkeys responded negatively to unequal reward distributions, e.g. they refused participation if they witnessed a conspecific obtain a more attractive food reward for equal effort, an effect amplified if the partner received such a reward without any effort at all. The effort effect, however, could not be replicated as clear in a later study [9]. Thus, although controversial, it seems that when tested in an exchange task, capuchin monkeys and chimpanzees seem to be sensitive at least to the unequal reward distribution [4, 5]. These results receive further support by a recent experimental study on cottontop tamarins (*Saguinus oedipus*) that found behavioural differences caused by unequal reward distributions in a cooperative problem solving task [10].

However, primates are not the only animals known to engage in cooperative actions (for review see [11]). Canids, for example, are known to engage in cooperative hunting (e.g. wolves, *Canis lupus* [12]; African wild dogs, *Lycaon pictus* [13]) and cooperative rearing of pups (e.g. wolves [14], African wild dogs [15, 16]; mongoose, *Suricata suricatta* [17]). Whereas dog-dog cooperation seems to be impaired by the domestication process [18, 19], dogs clearly show

effective, complex and elaborate cooperation with humans (e.g. gun dogs, assistant dogs)[20]. The continuous change in initialization of actions found in guide dogs and blind persons has not been reported among wolves. Co-working between dogs and humans often includes more than one dog interacting with humans e.g. in hunting. As dogs show high sensitivity to elements of human behaviour that are directed both towards them and to others [21, 22], and some understanding of human intentions ([23] but see [24]), we predict that dogs may respond differently when owners distribute rewards unequally among their dogs, this includes asking for different efforts from the dogs for the same reward. We expect that dogs will at least show some primitive version of inequity aversion such as reacting to the presence or absence of rewards (also see [25]). Paying close attention to other dogs and adjusting their behaviour accordingly has already been demonstrated in several other studies [21, 22].

Results

The aim of this study was to investigate whether domestic dogs are influenced by the inequity of rewards that were received for the same action in pairs of familiar dogs when working with the same experimenter. In a similar manner to the primate studies [4, 9], the experimenter requested the dogs to perform a certain action (instead of having to exchange a token for food, the dogs were asked to give their paw) in order to gain a food reward. Giving the paw is a command often trained rather for fun than for obedience (e.g. like sit, come), which means that it is usually carried out in connection with a reward and in a relaxed situation. Thus, like exchanging a token in the primate studies, giving the paw is probably not very effortful for the dog in terms of energy invested. However, in pilot studies we found that most dogs would stop giving the paw after 15-20 times if not rewarded.

For giving the paw to the experimenter on command (e.g. the hand of the experimenter was held out to the respective dog and the command ‘paw’ was spoken; the experimenter avoided any other communication with the dogs), 1) the subject and the partner received the same low-value reward (baseline condition: Equity Test (ET)), 2) the subject received a lower-value reward than its partner (Quality Inequity Test (QI)), 3) the subject received no reward while the partner received the low value reward (Reward Inequity Test (RI)) or 4) both dogs received the low-value reward but the partner did not have to give the paw in order to receive this reward (Effort Control (EC)). In addition, each dog was tested without a partner in an asocial test session consisting of an assessment condition followed by a no reward control condition. In the

assessment condition, the subject received a low value reward for giving the paw. This tested whether the dogs would, in general, give the paw to an unfamiliar person 30 times. With the no reward control condition (NR) we tested how long the dogs would continue giving the paw without a reward (for a summary of the conditions please see table 1).

Both the high value reward (sausage) and the low value reward (dark bread) were present and clearly visible for each dog in all conditions including the assessment and control sessions. Each test session consisted of a series of 30 trials, in each of which the partner performed immediately before the subject (or until the subject refused to work). The asocial control was conducted according to Bräuer and colleagues [6] to control also for the movement of the food (see procedures for details and figure 1 for a sketch of the general set-up). The order of the four social conditions and the two asocial conditions deviated from a fully counterbalanced design in that we randomized the sequence of the conditions across subjects, but never started with the reward inequity test or the no reward condition. This latter restriction was administered to avoid frustration by the subject. This is likely if an animal were put into a completely novel situation, commanded by an unfamiliar person and then not rewarded for the commanded action. Thus, we first established the testing situation with conditions where both animals were rewarded before testing any of the no reward condition. The asocial control was conducted for half of the dogs before and for half of the dogs after the social conditions.

Overall, the 29 dogs (see supplementary Table 1 for breed, sex and sequence of test sessions) differed in the number of trials in which they continued to give the paw to the experimenter in the four test sessions (Friedman; $FR = 35.115$; $N = 29$, $p < 0.0001$; corrected $p < 0.01$; Figure 2). A priori planned comparisons revealed that subjects refused to give the paw to the experimenter earlier in the reward inequity condition (RI) compared to the baseline condition (ET)(Dunn's Multiple comparisons test: $p < 0.001$; corrected $p < 0.01$). None of the other two test conditions differed significantly from the baseline condition (Dunn's Multiple comparisons test: ET – QI: $p > 0.05$; ET – EC: $p > 0.05$). Do dogs always refuse to give the paw when no reward is provided independently of the presence or absence of a rewarded partner? We found that partner presence makes a difference: subjects would stop significantly earlier to obey the command if a partner was present compared to the asocial control (RI – NR: Wilcoxon- matched pairs test: $N = 25$ (4 ties), $T+ = 84$, $p = 0.034$, corrected $p < 0.05$). The partner receiving a reward thus seemed a crucial factor responsible for refusing to give the paw in the reward inequity test (Figure 2).

In addition to the number of trials during which the subject continued to obey the command, we analyzed the hesitation or willingness of the subject to do so. In our experiment, the experimenter would repeat the command up to 10 times. If the subject did not give the paw on command during this time then the session was terminated (see experimental procedures in the supplementary information for details). When we calculated the average number of times per trial that the experimenter had to prompt the subject to give the paw before it obeyed we found an overall significant difference between the four experimental conditions (Friedman; $Fr = 38.011$; $N = 29$, $p < 0.0001$, corrected $p < 0.01$; Figure 3). Planned posthoc comparisons revealed the same difference as before with only RI differing significantly from the baseline condition (Dunn's multiple comparisons test, ET - RI: $p < 0.001$, corrected $p < 0.01$; ET - QI: $p > 0.05$; ET - EC, $p > 0.05$). Moreover, like in our first measurement, the reward inequity condition also differed significantly in the average number of times per trial the command had to be repeated compared to the asocial control condition (RI - NR: Wilcoxon-matched pairs test: $N = 28$ (1 tie); $T+ = 362$; $p = 0.0001$; corrected $p < 0.01$), suggesting that the subjects were less willing to give the paw to the experimenter when their partner was rewarded for the same action compared to not being rewarded when alone. The same results were found if all commands given (to sit up and to give the paw) were combined for the analyses.

If animals react to the inequity of the reward distribution, one would further expect that they check more often what the other animal gets. Accordingly, we analyzed whether subjects looked more often at their partner in one or the other condition. However, we found no significant difference between the four conditions (Friedman; $Fr = 2.668$; $N = 28$, $p < 0.445$). Finally, we analyzed whether subjects showed more signs of distress (defined as the average number of scratching, yawning, licking the mouth, avoiding the gaze of the partner per trial) in the inequity conditions compared to the control condition. We found an overall significant difference between the four experimental conditions (Friedman; $Fr = 15.561$; $N = 29$, $p < 0.0014$, corrected $p < 0.01$). Posthoc comparisons revealed a significant difference between the baseline and the reward inequity condition (Dunn's multiple comparisons test, ET - RI: $p < 0.01$, corrected $p < 0.05$), but no difference between the other two conditions and the baseline (Dunn's Multiple comparisons test, ET - QI: $p > 0.05$; ET - EC: $p > 0.05$). The subjects also were more stressed in the reward inequity condition compared to the asocial control condition (Wilcoxon matched pairs test, RI - NR: $N = 29$; $T+ = 324.0$; $p < 0.021$; corrected $p < 0.05$), suggesting that not getting a reward if

the partner is rewarded is more stressful than not getting a reward in the absence of a rewarded dog.

So far, these results suggest that the dogs are sensitive to an unequal reward distribution rather than, or at least much more than, to a difference in quality or effort. However, it is possible that the animals reacted merely to the presence of the partner in the reward inequity condition and not to the partner receiving food. Therefore, in a second experiment, we tested additional dogs in two further conditions, controlling for the presence of the partner. For giving the paw to the experimenter on command, 1) the subject and the partner both received no reward (baseline: Social Control (SC)) or 2) the subject received no reward while the partner received the low value reward (Reward Inequity Test (RI)).

The general design of the experiment remained the same as the first experiment with 1) both the high value reward (sausage) and the low value reward (dark bread) were present and clearly visible to each dog in both conditions, 2) each test session consisting of a series of 30 trials (or until the subject refused to work), in each of which the partner performed immediately before the subject and 3) the incorporation of the movement of the food (see procedures for details). The social control was conducted for half of the dogs before and for half of the dogs after the reward inequity test.

Overall, we found a trend towards a difference with the 14 tested dogs refusing to give the paw earlier in the reward inequity condition (RI) compared to the social control condition (SC)(Wilcoxon-matched pairs test: $N = 10$ (4 ties), $T+ = 10.0$, $p = 0.08$, Figure 4). Moreover, we found that the dogs hesitated significantly longer when obeying the command to give the paw in the reward inequity condition compared to the social control condition (Wilcoxon- matched pairs test: $N = 14$, $T+ = 99.0$, $p = 0.0017$, Figure 5). They also looked at the partner significantly more often and were more stressed in the reward inequity condition compared to the social control condition (Wilcoxon- matched pairs test: Looking at the partner: $N = 14$, $T+ = 96.0$, $p = 0.004$; Stress signals: $N = 14$, $T+ = 96.5$, $p = 0.0031$), even though food was present and moved in both conditions. These results strongly suggest that the dogs react to the fact that the partner received the food and not just to the presence or absence of a partner dog.

Discussion

Together, the results of experiment 1 and 2 provide the first evidence for the presence of sensitivity towards an unequal reward distribution in a non-primate species. The dogs refused earlier and hesitated longer to obey human commands, showed more stressed behaviour in the social condition compared to the asocial control condition in the first experiment. In the second experiment, the dogs also showed a tendency to a higher refusal rate, a significantly longer hesitation, higher stress levels and increased looking at the partner when the partner was rewarded and they themselves not.

In regard to the original non-human primate studies on inequity aversion, several alternative explanations have been suggested to explain the behavior of the animals. First, it has been argued that the monkeys reacted towards the presence of the high-value food reward when receiving a low-value reward rather than the fact that the partner received the high-value reward [8, 23], even though this explanation was later ruled out by an experiment that controlled for the mere presence of high-value food [9]. In our experiment, both the low and the high-value reward were always present and clearly visible to both animals. Thus, it is unlikely, that visibility of the high-value reward accounts for our results.

Another alternative hypothesis suggested that the monkeys were frustrated by receiving a low-value reward after having received a high-value reward in a previous session [7, 8]. It had been shown that animals react differently e.g. show frustration effects when they expect a certain outcome, so that absence of the expected reward results in delays [24, 25] or reduced preference [24-27]. This frustration effect (also called ‘contrast’ effect) rather than aversion to inequity might explain the refusal of the less preferred reward in studies where monkeys received a high-value reward before being tested with a low-value reward [7, 8], but a recent study using the original token exchange task confirmed previous results of inequity aversion even after controlling for the frustration effect [9]. In both our experiments, all ‘no reward control’ conditions were run after an assessment condition or warm-up trials so that all ‘no reward’ and all ‘reward inequity’ conditions were preceded by a condition where the subject received low-value rewards for giving the paw. Consequently, if the observed aversion to the unequal reward distribution could be explained by the frustration or contrast effect, we would not have expected any difference between the reward inequity condition and both the asocial and social control conditions. In the first experiment none of the subjects received any high-value rewards except once at the beginning of every test condition, thus a shift from high- to low-value reward cannot explain the results of the first experiment either.

Interestingly, our results differed from results of the primate studies in that we found no indication for sensitivity towards the quality of the food reward and the effort involved. Primates react to the quality of food, not just the presence/absence, and show more negative reactions than the dogs in this study [2, 9]. The dogs' lack of sensitivity is also surprising in light of many studies demonstrating that a violation of expectancy of a certain food reward leads to a higher rejection rate in several species [24, 27]. Although all owners whose dogs participated in this study confirmed that their dogs are more motivated to work if they receive sausage rather than bread as a reward, the dogs continued to give the paw for a low value reward both in the social and the asocial assessment session, even when the high value reward in front of them. There might, in fact, be several processes at work that could explain why we found no violation of expectancy effect in this study and why the dogs did not react to the quality inequity condition: 1) all tested dogs were well trained used to work on a daily basis with their owners. This training effect might override the violation of expectancy effect, prompting the dogs to continue working as long as they receive a reward at all. Also the fact that they had to 'work' for the reward might have enhanced the quality of the reward. 2) In the social conditions, working next to a partner might have a facilitation effect, increasing the motivation of the subject to continue working even if only the partner is receiving the high value reward and not they themselves. And possibly most importantly, 3) that the presence of the rewards themselves was such a strong motivator that they obscured the results of any quality inequity assessment by the subjects. Further studies have to be conducted to reveal which of these explanations maybe responsible for the lack of sensitivity for the quality of the reward that was observed in this study. Until we can answer these questions, it would be highly speculative to discuss whether this lack of sensitivity to the quality of the reward is a specific feature of domestic dogs or one of canines in general. Of course, it would be tempting to assume that a domesticated species like the dog is less likely to react negatively than a non-domesticated species. However, attempting to answer this difficult question would require devising experiments in which the dogs may behave more like the primates that have been tested so far.

The strong motivating effect of the presence of rewards might explain also the lack of sensitivity towards differential effort invested by the subject and its' partner. Alternatively, the insensitivity to the effort distribution and the food quality may be interesting in light of the evolution of cooperation. It has been argued that the psychological mechanism necessary for inequity aversion in regard to the invested effort and the reward, requires animals to 'perceive a

relation between relations, i.e. to compare the relation between its own effort and reward (one token for one cucumber) with the relation between the partner's effort and reward (one token for one grape, or no effort for one grape)[8]. So far, it has only been shown that humans, chimpanzees and, to a lesser extent, baboons are able to solve tasks that require the perception of relations between relations [28, 29]. As a consequence, it is possible that dogs lack the cognitive abilities to show sensitivity to the outcome in relation to the effort invested. It is possible that sensitivity towards being rewarded or not may be the precursor to cognitively higher-level forms of inequity aversion.

The fact that the subjects refused earlier and hesitated longer to obey the command to give the paw to the experimenter when the partner received a reward but they themselves did not compared to the baseline condition as well as to the asocial and social control conditions suggests that dogs are sensitive to an unequal reward distribution. The lack of sensitivity toward the quality and the effort invested, however, also highlights the differences towards inequity aversion demonstrated in primates. Also, in contrast to the primates, the dogs never rejected food. Thus, also the dogs were only responsive to disadvantageous inequity aversion (in contrast to advantageous inequity aversion characterizing humans) and were not willing to pay a cost by rejecting unfair offers (as is characteristic also of nonhuman primates), there is a fundamental difference in the behaviour of the primates and the dogs. The observed sensitivity towards the presence and absence of rewards may thus present a precursor of more sophisticated forms of inequity aversion. Further questions are raised concerning the evolutionary origin of at least a primitive form of inequity aversion – is it specific for primates and domesticated species working with humans or is it more general feature present in other social species as well? In the latter case, did it evolve several times or does it have a very old origin and gradually developed into more and more sophisticated sensitivity to efforts and pay-offs of joint interactions? Further studies thus need to determine 1) whether this ability is restricted to human-related species or to animals that cooperate with each other under natural conditions or rather a widely distributed phenomena in the animal kingdom and 2) whether the lacking sensitivity towards the invested effort of the partner is specific to dogs either resulting from their evolutionary history of domestication or their developmental training by humans.

Experimental procedures

A precondition for participation in the study was that the dogs had to know the command ‘to give the paw’. Details of the training and the experimental procedures are given in the supplementary methods. Each subject was tested as subject and partner in all conditions. The equity test (ET) was a baseline test in which both the subject and the partner performed for a low-value reward (dark bread). In the quality inequity test (QI), which determined their response to a high- and low value reward distribution, the partner first performed for a high-value reward (sausage) followed by the subject asked to perform for a low-value reward (dark bread). In the reward inequity test (RI), which determined their response to an unequal presence of reward, the partner first performed for a low-value reward (dark bread) followed by the subject asked to perform but receiving no reward. In the effort control test (EC) the partner was initially handed a low-value reward without having to perform for it (dark bread as a gift), after which the subject had to perform to receive the low-value reward (dark bread).

In order to control that the dogs did react to the movement of the food in the social condition rather than to the partner being rewarded, as has been claimed for chimpanzees [6], the asocial control sessions included the movement of the food i.e. the experimenter showed the food to the dog, moved the arm (food in the hand) towards the position where the other dog sat or would sit during the social conditions, opened the palm, closed the palm, moved the arm back and put the food back in the bowl in a way invisible to the subject before the subject was asked for the paw but did not receive a reward.

Each dog served as partner and subject in their respective dyad; the sequence was randomly chosen. The first subject was tested in all conditions before the roles were reversed. We carried out two test sessions per day with a 15 minute break between them. The sequence of the four test sessions was counterbalanced between subjects with the only condition that it never started with the RIQ session. This condition assured that dogs in the asocial no reward condition and in the RIQ condition were downshifted equally (e.g. received a low-value food reward in the session beforehand). The assessment and the asocial control sessions were either carried out before or after the test sessions in the same sequence.

In experiment 2, each of the two test sessions consisted of a series of 20 warm-up trials (both subjects received the low value reward for giving the paw on command) and 60 experimental trials, with trials alternating between the partner and the subject such that each individual received 40 trials per session (or until the subject refused to work) and the partner always performed immediately before the subject. In the social control condition (SC), the subject and

the partner were both asked to give the paw on command but neither of them was rewarded. The reward inequity condition was identical to the one in the first experiment. Again, to control for the movement of the food, the food was visibly lifted in front of the dogs but returned to the food bowl in the trials when they were not rewarded. The order of the two sessions was counterbalanced across subjects.

All tests were two tailed and alpha was set at 0.05; trends are reported for $0.1 > \alpha > 0.05$. When we analyzed subsets of data (comparing the RI and the NR condition), the corresponding probabilities were corrected using a sequential Bonferroni procedure [30]. All results remained significant at the 5% level after the correction. Inter-observer reliability for the dogs' behaviour, based on coding 10 sessions of different dogs from video records, was calculated as Cohen Kappas: giving the paw: 0.97; looking at the partner: 0.93; appeasement signals (yawning, scratching, licking the mouth, avoiding the gaze): 0.89.

Further details of the training and the experimental procedures are given in the supplementary methods.

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Figure legends

Figure 1: Photos of the experimental set-up. The experimenter avoided eye contact with the dogs. The owner was standing behind the dogs.

Figure 2: The box plots show the number of trials the subject gave the paw to the experimenter in the four different test conditions and the non-social control condition without reward. Shaded boxes represent the interquartile range, bars within shaded boxes are median values and whiskers indicate the 5th and 95th percentile. ET = equity test, both animals receive a low-value reward; QI = quality inequity test, where the partner initially performed for a high-value reward followed by the subject asked to perform for a low-value reward; RI = reward inequity test, where the partner initially performed for a low-value reward followed by the subject performing but receiving no reward; EC = effort control, where the partner was initially handed a low-value reward without having to perform for it, after which the subject had to perform to receive the low-value reward. NR = asocial control, where the animal was tested alone and received no reward.

Figure 3: The box plots show the average number of times per trial the experimenter had to ask the subject to give the paw in the four different test conditions and the non-social control condition without reward (NR). Shaded boxes represent the interquartile range, bars within shaded boxes are median values and whiskers indicate the 5th and 95th percentile. For description of the shortcuts please see figure legend 1.

Figure 4: The box plots show the number of trials the subject gave the paw to the experimenter in the two test conditions of experiment 2 (RI = reward inequity condition; SC = social control condition). Shaded boxes represent the interquartile range, bars within shaded boxes are median values and whiskers indicate the 5th and 95th percentile.

Figure 5: The box plots show the average number of times per trial the experimenter had to ask the subject to give the paw in the two experimental conditions (RI = reward inequity condition; SC = social control condition). Shaded boxes represent the interquartile range, bars within shaded boxes are median values and whiskers indicate the 5th and 95th percentile.